REVIEW

Evolution of the amygdaloid complex in vertebrates, with special reference to the anamnio-amniotic transition

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Abstract

Numerous studies over the last few years have demonstrated that the amygdaloid complex in amniotes shares basic developmental, hodological and neurochemical features. Furthermore, homologous territories of all the main amygdaloid subdivisions have been recognized among amniotes, primarily highlighted by the common expression patterns for numerous developmental genes. Thus, derivatives from the lateral pallium, ventral pallium and subpallium constitute the fundamental parts of the amygdaloid complex. With the development of new technical approaches, study of the precise neuroanatomy of the telencephalon of the anuran amphibians (anamniotes) has been possible. Current embryological, hodological and immunohistochemical evidence strongly suggests that most of the structures present in amniotes are recognizable in these anamniotes. These investigations have yielded enough results to support the notion that the organization of the anuran amygdaloid complex includes subdivisions with their origin in ventral pallial and subpallial territories; a strong relationship with the vomeronasal and olfactory systems; abundant intra-amygdaloid connections; a main output centre involved in the autonomic system; recognizable amygdaloid fibre systems; and distinct chemoarchitecture. Therefore, the new ideas regarding the amygdaloid evolution based on the recent findings in anamniotes, and especially in anurans, strongly support the notion that basic amygdaloid structures were present at least in the brain of ancestral tetrapods organized following a basic plan shared by tetrapods.

Key words amygdala; anurans; development; hodology; homology; neurochemistry; pallium; subpallium; tetrapods.

Introduction

The study of the group of nuclei in the ventrolateral telencephalon that constitute the amygdaloid complex (AC) of vertebrates is currently the main research topic in many laboratories because it has been implicated in a variety of functional systems directly involved in the final behavioural response of the animal (LeDoux, 1995, 2000). A general feature that has emerged in recent research is that the AC is much more complicated than previously thought, and thus it seems essential to know the precise boundaries of its components and their characterization in terms of connectivity and chemoarchitecture before we can draw conclusions on the possible implications of each subdivision in disorders of emotional and social behaviour.

The organization of the AC in different amniotic vertebrates (reptiles, birds and mammals) has been profusely studied over recent decades and, as a result, a common basic pattern of organization has been recognized that most probably reflects shared functional roles. In parallel, investigation regarding the anatomy of the telencephalon of anamniotes (amphibians and fish) provided little detailed information on the organization of its subdivisions. However, with the development of new technical approaches, the existence of homologous territories to the amygdaloid components in anamniotes has been recently investigated. In particular, current research on the putative AC of anuran amphibians has highlighted the presence in these anamniotes of subdivisions in the basal telencephalon that are readily comparable with AC components of amniotes, in terms of development, hodology and chemoarchitecture (for a review see Moreno & González, 2006). Therefore, as the amphibian ancestors are known to have given rise to the reptile-like vertebrates in the Carboniferous, the new data, in an evolutionary context, provide a new perspective about the evolution of the AC in tetrapods. The use of this comparative approach seems essential to elaborate solid hypothesis concerning the anatomical and functional organization of the amygdaloid complex.

In order to characterize particular brain regions and evaluate their possible evolution, a 'sequential approach', i.e. step by step, seems to be the most valid strategy. Thus, developmental,

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topological (including analysis of form, structure and cytoarchitecture), hodological and functional steps in the investigation are used to confirm the entity of a given brain region and allow its comparison with its counterparts in other vertebrates, contributing to understand its evolution.

Some authors have interpreted the AC as an extended continuum within the basal telencephalon that rostrally reaches the caudal tip of the shell portion of the nucleus accumbens (Alheid et al. 1995; Martínez-García et al. 2002). In contrast, based on the heterogeneous origin, chemoarchitecture and connectivity of the AC, other authors have proposed that it represents the sum of different, unrelated anatomical structures, with pallial and subpallial derivatives, belonging to four different functional systems: the main olfactory, the accessory olfactory (vomeronasal), the autonomic and the frontotemporal cortical systems (Swanson & Petrovich, 1998; Puelles et al. 2000). However, recent developmental, hodological and neurochemical data have shown striking similarities between the complicated AC of mammals and the relatively simpler AC of reptiles and anurans, suggesting that all its parts have evolved following common traits, more as a whole than as the sum of unrelated structures with different origins. Nevertheless, it should be noted that significant differences were also found in the organization of the AC among vertebrates. For instance, in the avian brain the presence of a huge dorsal ventricular ridge (of uncertain comparative significance), the relatively poorly developed olfactory system and the virtual absence of a vomeronasal system (Reiner & Karten, 1985) have hindered the identification of the avian amygdaloid components. In turn, the lack of cortical structures in anamniotes has resulted in the lack of these amygdaloid regions and it has also hindered the precise identification of other amygdaloid nuclei (Moreno & González, 2006).

The current view of the AC in tetrapods considers pallial and subpallial components. Thus, the 'pallial amygdala' comprises derivatives of the lateral and ventral pallium, whereas the 'subpallial amygdala' consists of derivatives of the lateral and medial ganglionic eminences (Puelles et al. 2000; Martínez-García et al. 2002; Moreno & González, 2006). This dual origin makes the AC a histogenetic complex area, with the morphogenetic and migratory process during development being extremely intense, which increases the complexity of the adult structure in all tetrapods (Puelles et al. 2000). In mammals, the pallial amygdala is composed of a superficial group of nuclei that shows a laminar organization and is called 'cortical amygdala' and a deep group of nuclei that form the 'basolateral amygdala'. In turn, the subpallial amygdala is formed by a striatal component, the central amygdala, and subpallial component, the medial amygdala, which most likely also contains pallial elements (Martínez-García et al. 2002; Medina et al. 2004). This basic *bauplan* is shared by reptiles and birds (Smith-Fernández et al. 1998; Puelles et al. 2000;

Martínez-García et al. 2002; Yamamoto et al. 2005; Abellán et al. 2006) and also by anuran amphibians (Moreno & González, 2006), as evidenced by the largely comparable expression patterns of different genes implicated in regional specification. However, it should be pointed out that although the main amygdaloid nuclei have been homologized across tetrapods (by means of different and multiple technical approaches) the non-mammalian amniotes and the anurans do not possess all the anatomical subdivisions present in mammals (Fig. 1).
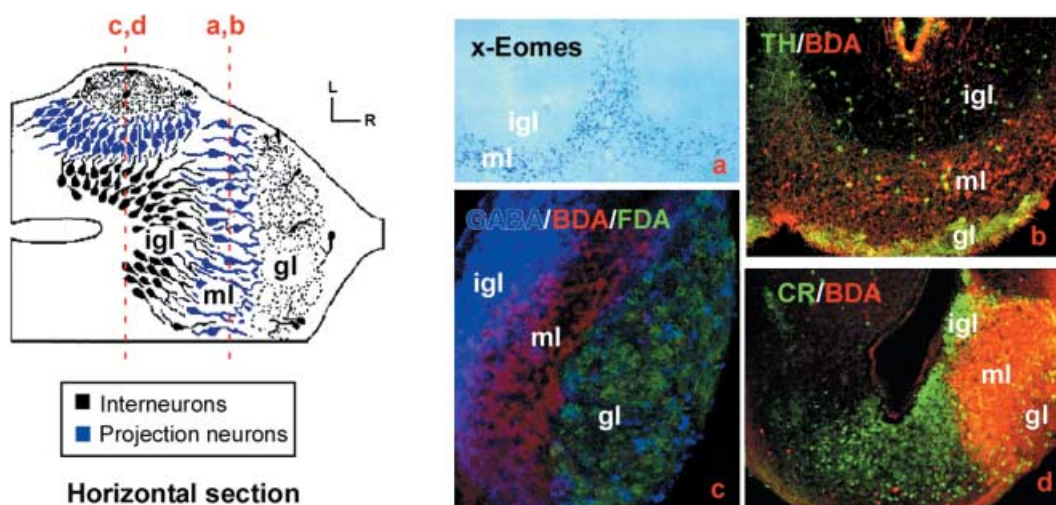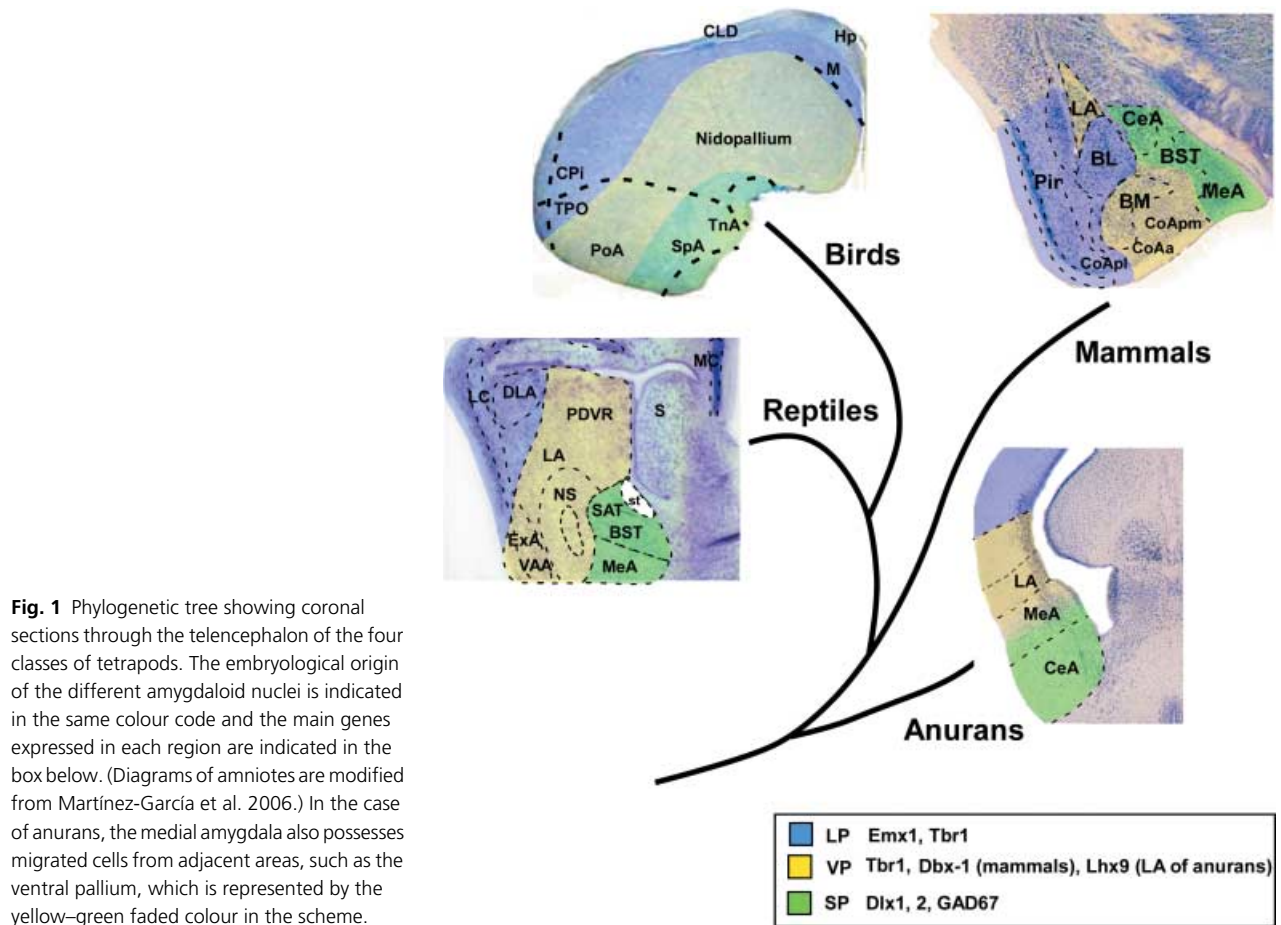
The existence of an AC with components that share embryological origin in all tetrapods has a major implication in the interpretation of the evolution of this structure in that the precursors of the amygdaloid nuclei are already present from anamniotes. In the following sections we will deal with the major characteristics that are now accepted as being shared in the organization of the AC in tetrapods. In addition, we will comment on the recent data from fish suggesting that the AC is recognizable in teleosts, reinforcing the idea that its crucial functional role has been conserved through evolution.

The amygdaloid functional systems in tetrapods: from connectivity to function

The amygdala is part of the phylogenetically conserved olfactory system

The olfactory system and in particular the olfactory bulbs are extremely conserved in vertebrate evolution in terms of embryological origin, neurochemistry, connectivity and function. In all tetrapods the olfactory bulbs are pallial structures that incorporate subpallial components (Puelles et al. 2000). In particular, the olfactory neurons projecting outside the bulbs are pallial cells, like all projection neurons in the cortex, whereas the interneurons originate in the subpallium. This situation has also been confirmed in anurans, in which the mitral neurons express pallial markers (Moreno et al. 2003), while the interneurons express subpallial markers and are thought to reach the bulbs probably following a migratory process similar to that of amniotes (Smeets & González, 2000; Boyd & Delaney, 2002; Brox et al. 2003) (Fig. 2).

A major part of the amygdala is an integral component of the olfactory and vomeronasal systems of the brain (Swanson & Petrovich, 1998; Halpern & Martínez-Marcos, 2003; Moreno & González, 2006), receiving large olfactory and vomeronasal projections in all tetrapods (Swanson & Petrovich, 1998; Moreno et al. 2005). In fact, the amygdala includes the main secondary vomeronasal and olfactory centres in the brain (Swanson & Petrovich, 1998). Thus, the organization of the main sensory inputs of the amygdala (vomeronasal and olfactory) is extremely conserved, at least in tetrapods, which is striking in view of the evolutionary distance between species. However, it should be noted

Fig. 1 Phylogenetic tree showing coronal sections through the telencephalon of the four classes of tetrapods. The embryological origin of the different amygdaloid nuclei is indicated in the same colour code and the main genes expressed in each region are indicated in the box below. (Diagrams of amniotes are modified from Martínez-García et al. 2006.) In the case of anurans, the medial amygdala also possesses migrated cells from adjacent areas, such as the ventral pallium, which is represented by the yellow–green faded colour in the scheme.

Fig. 2 Schematic drawing of a horizontal section through the olfactory bulbs of anurans illustrating the layered arrangement of interneurons and projection neurons. (a–d) Photomicrographs of transverse sections at the levels indicated in the schematic drawing, illustrating: (a) *in situ* hybridization in the main olfactory bulb of *Xenopus laevis* showing the expression of the gene *x-Eomes* in the mitral cells; (b) main olfactory bulb of *Rana perezi* showing in red projection neurons retrogradely labelled from the amygdala and in green tyrosine hydroxylase-immunoreactive interneurons; (c) accessory olfactory bulb of *Rana perezi* showing in blue GABA-immunoreactive interneurons, in red projection neurons retrogradely labelled from the medial amygdala and in green anterogradely labelled vomeronasal fibres and terminals; (d) accessory olfactory bulb of *Xenopus laevis* showing in red projection neurons retrogradely labelled from the medial amygdala and in green calretinin-immunoreactive interneurons.

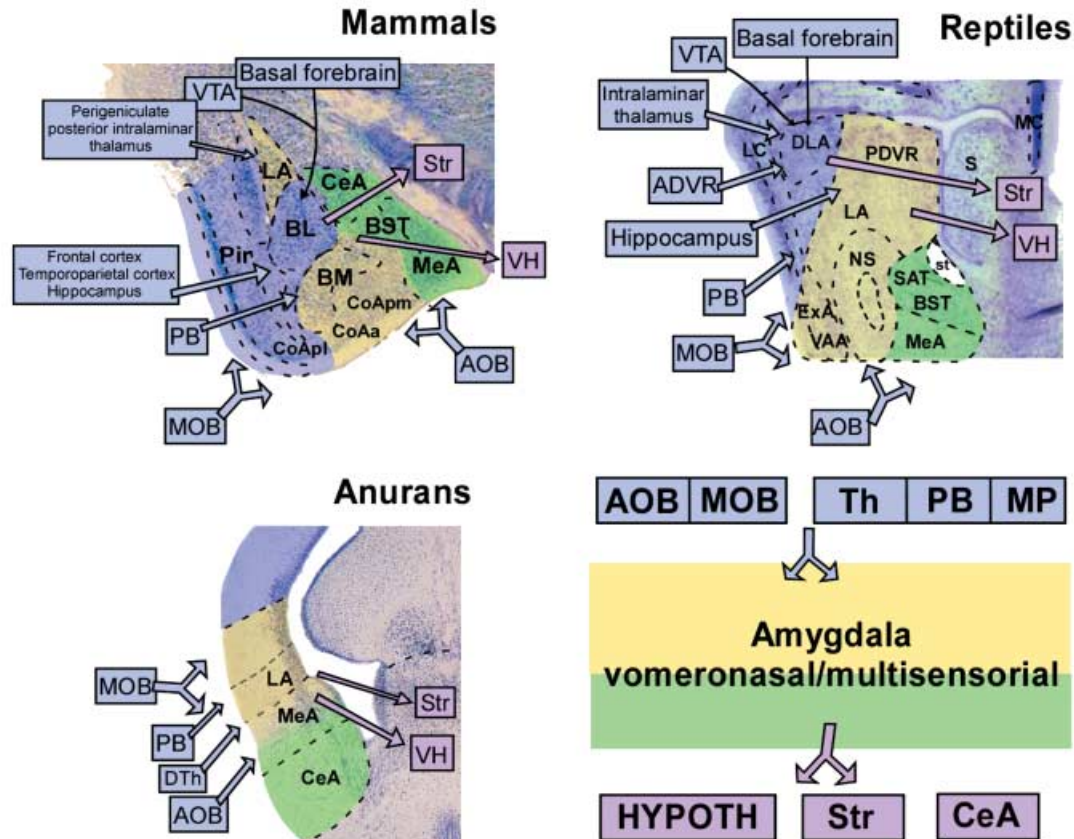Multisensorial inputs to the amygdala: the olfactory/vomeronasal system in tetrapods

Fig. 3 Drawings over representative coronal sections through the amygdaloid complex and a diagram (lower right) illustrating its main connections in relation to olfactory vomeronasal and multimodal information. (Diagrams of amniotes modified from Martínez-García et al. 2006.)

that in the avian brain the absence of a vomeronasal system and the important reduction of the olfactory system hamper the identification of the pallial amygdala.

The vomeronasal amygdala
In mammals, the vomeronasal information passes via the accessory olfactory bulb (AOB) to the 'vomeronasal amygdala', i.e. the medial (MeA) and the cortical postero-medial amygdala (CoApm) (Swanson & Petrovich, 1998). The CoApm is a cortical amygdaloid area that displays important bidirectional connections with the AOB and a minor relationship with the lateral hypothalamic area (Canteras et al. 1992; Risold et al. 1997). In addition, it projects to other telencephalic centres, primarily to other amygdaloid subdivisions (Canteras et al. 1992; Swanson & Petrovich, 1998; Martínez-García et al. 2002). The MeA receives a massive unidirectional input from the AOB and a restricted input from the main olfactory bulb (MOB; Scalia & Winans, 1975; Lehman & Winans, 1982; Canteras et al. 1995) and projects massively to the hypothalamus, especially to the ventromedial nucleus to modulate repro-ductive and defensive behaviours (Canteras et al. 1994, 1995; Risold et al. 1997; Choi et al. 2005). In reptiles and anurans the existence of a well-developed 'vomeronasal

amygdala' has been reported (Scalia et al. 1991; Lanuza & Halpern, 1998; Moreno & González, 2003). By contrast, this system in birds has not been described and therefore no vomeronasal amygdaloid nuclei have been reported in the pallial amygdala (Martínez-García et al. 2006). However, the subpallial nucleus taeniae (TnA) has been traditionally considered, based on its olfactory input, to be the avian counterpart of the mammalian MeA (Reiner & Karten, 1985; Martínez-García et al. 2006). In reptiles the vomeronasal information is relayed in the AOB and reaches pallial areas (the nucleus sphericus) and a subpallial nucleus (the medial amygdala) that have been compared with the amygdaloid parts of similar origin in the vomeronasal amygdala of mammals (Lanuza et al. 1998). Unlike the case in amniotes, in anurans the MeA constitutes the only secondary vomeronasal centre in the forebrain and projects heavily to the ventral hypothalamus (Moreno & González, 2003, 2005b; Moreno et al. 2005). Thus, in all tetrapods the main secondary vomeronasal brain areas belong to the AC, but in amniotes this information reaches cortical and subpallial structures, whereas in anurans the only vomero-nasal area has a subpallial origin, although also possesses migrated cells from adjacent areas, such as the ventral pallium (Moreno & González, 2006, 2007) (Fig. 3). This is in line with

the notion of the total lack of cortical structures in the brain of anamniotes (Bruce & Neary, 1995; Striedter, 1997).

The olfactory/multisensorial amygdala

In their review of the organization of the AC of mammals into functional systems, Swanson & Petrovich (1998) proposed the existence of two distinct multisensorial systems: the frontotemporal amygdaloid system and a main olfactory amygdaloid system. However, in other vertebrates such a subdivision has not been recognized and it seems more appropriate to consider only one 'multisensorial amygdala', which certainly receives major olfactory information but also thalamic and brainstem inputs (Moreno & González, 2006).

In mammals, taken together, the olfactory/multimodal amygdaloid system consists of distinct cortical and deep amygdaloid areas. The cortical areas include the anterior cortical amygdala (CoAa), the posterolateral cortical amygdala (CoApl) and the cortex–amygdala transition area (CxA). In turn, the deep pallial areas (named, as a whole, the basolateral amygdala) include the basolateral (BL), basomedial (BM) and lateral (LA) nuclei (Swanson & Petrovich, 1998). Notably, the lateral nucleus, included in the frontotemporal functional system (Swanson & Petrovich, 1998), is the major sensory receptive area (LeDoux et al. 1990; Savander et al. 1997) and conveys sensory information to other amygdaloid nuclei for further processing (Pitkänen et al. 1995) and, thus, it is a very important component of the multimodal amygdala strongly implicated in the emotional behaviour (LeDoux, 2000). In the avian amygdala, the important reduction of the olfactory system has hindered the identification of the amygdaloid olfactory components. However, recent studies have postulated that the avian amygdala includes lateropallial olfactory cortices, the CPi, comparable with the COApl. In turn, the lateropallial structures of the avian brain deep to the CPi would be the putative homologues of the BL amygdala. In the ventral pallium, birds would posses only deep ventropallial amygdaloid nuclei, probably to be the counterparts of the BM and LA (Martínez-García et al. 2006).

Studies conducted in several species of reptiles (Martínez-García et al. 1991; Lanuza & Halpern, 1998; Lanuza et al. 1998) have identified the presence of a multimodal association area comparable with the mammalian basolateral complex. Two cortical (superficial and layered) structures in the caudal telencephalon were seen to receive a massive projection from the MOB, whereas a deep area receives multiple inputs including non-chemosensory afferents from the thalamus and telencephalic sensory centres, highly processed sensory information from the dorsal cortex, olfactory information from the (ventrocaudal) lateral cortex, and vomeronasal inputs from the nucleus sphericus. In addition, all this information is relayed to the ventromedial hypothalamus through the stria terminalis (Hoogland & Vermeulen-Vanderzee, 1995; Lanuza & Halper,

1997; Lanuza et al. 1997, 1998; Martínez-Marcos et al. 1999).

The anuran counterpart of the mammalian olfactory/multimodal amygdala, with a ventropallial origin, is the lateral amygdala (LA; Moreno & González, 2004; Moreno et al. 2004), which receives, directly or indirectly, olfactory, visual, auditory, somatosensory, vomeronasal and gustatory information. Therefore, in the anuran LA convergence of chemical (odours) and non-chemical (multisensory information) stimuli would occur (Moreno & González, 2003, 2004; Moreno et al. 2005). Convergence of projections from the vomeronasal and olfactory systems would account for an association of pheromones with odours, thus resulting in an emotional labelling of odours, conferring a predictive value to odours and allowing the animal to anticipate its reaction to the pheromone (Halpern & Martínez-Marcos, 2003). In addition, afferents from the thalamus would associate chemical (pheromones and odours) with non-chemical stimuli, as well as different non-chemical stimuli among them. All this suggests that the anuran amygdala plays an important role in the emotional labelling of any kind of novel stimuli as either attractive or aversive, in the 'emotive memory', thus conditioning the animal behavioural response based on its previous experiences (LeDoux, 1995, 2000).

Concerning the possible existence of a lateropallial component of the amygdala in anurans, this structure should have, in addition to the olfactory input, an important bidirectional connection with the striatum and important cholinergic and dopaminergic innervation (Martínez-García et al. 2002, 2006), both lacking in the anuran lateral pallium (Marín et al. 1998a; Moreno et al. 2004).

The multimodal integration that occurs in the AC is the basis for the acquisition of the 'emotional memory' and it has as its final response the 'emotional behaviour', i.e. responses that occur to warrant the survival of individuals and their species as, for instance, in defence against danger, in the interaction with sexual partners or in fighting with an enemy (LeDoux, 2000; Paré, 2003). It allows the association of different stimuli that are important in terms of survival, reproduction, etc., with emotions occurring at the same time. This results in an emotional labelling of odours and pheromones with important somatosensory and autonomic components (LeDoux, 1995, 1996) (Fig. 3).

The autonomic amygdala: conservation of centres with essential functions

This component of the amygdala, the central amygdala (CeA), constitutes the main integrative centre in the AC. In all tetrapods studied it receives a wide range of sensory information from other amygdaloid regions and ascending thalamic and brainstem inputs. All this information will modulate the behavioural responses that could be the sum of the stimuli from other amygdaloid nuclei. Thus, the other amygdaloid systems project directly to the CeA
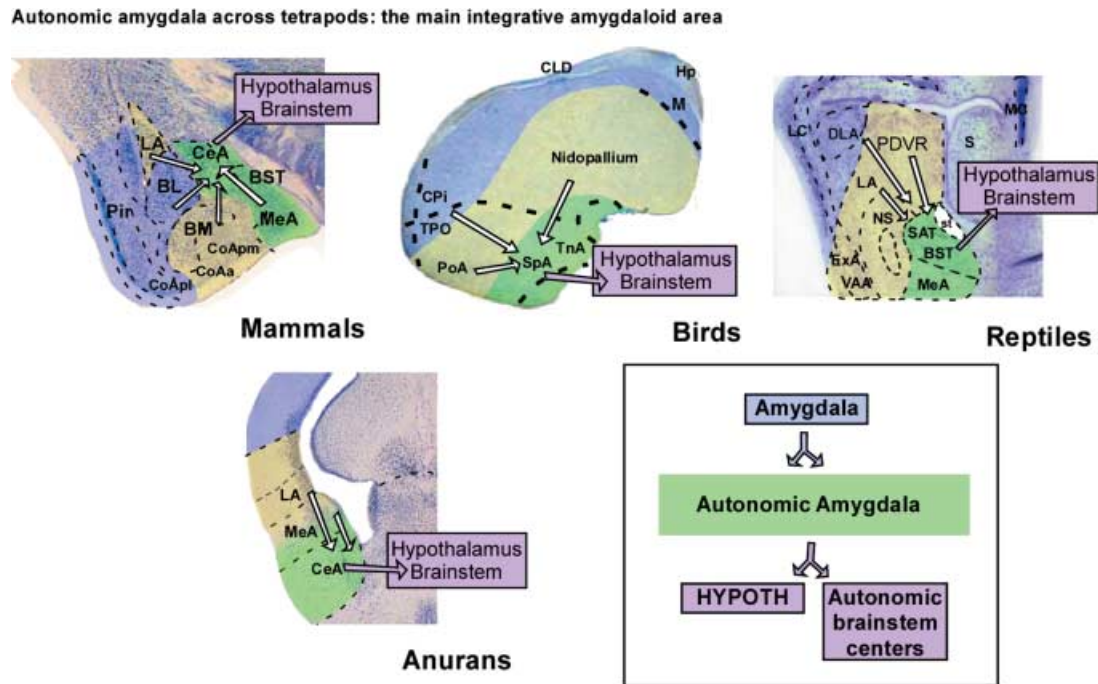
Fig. 4 Annotated coronal sections through the amygdaloid complex and a diagram (lower right) illustrating the principal intra-amygdaloid connections and the connections between the amygdala and the autonomic system. (Diagrams of amniotes are modified from Martínez-García et al. 2006.)

carrying different environmental stimuli (vomeronasal, olfactory, auditory, gustatory, etc.) that the CeA integrates. By means of its projections to the main autonomically related centres (including the mesencephalic tegmentum, the solitary tract, the parabrachial area and the lateral hypothalamic area) the CeA modulates the autonomic, somatic and endocrine responses that coursed along with the behavioural response. In addition, the CeA has been linked to the integration of emotional and motor components of behaviour, and to the mediation of conditioning-orientated responses (Gonzales & Chesselet, 1990; Han et al. 1997), behavioural responses to nociceptive and conditioned aversive stimuli and visceral pain (Finn et al. 2003; Han & Neugebauer, 2004), as well as behavioural responses to stressful stimuli (Saha et al. 2000).

The identification in all tetrapods of an autonomic amygdala is relatively easy and it seems that homologous components to the mammalian CeA represent a conserved evolutionary entity (Fig. 4). The CeA constitutes a striatal component (in origin) that is an integrative area and possesses long descending projections to autonomic centres (Moreno & González, 2006). In addition, in the different tetrapods it has been involved in mediating many autonomic, somatic, endocrine and behavioural responses. The conservation of this system in evolution is of important significance in that the autonomic amygdala constitutes the link between the environmental stimuli received by the animal and the correct behavioural response based on previous experiences, association of apparently unrelated stimuli, learned behaviours, etc.

(mediated by its connections with the other amygdaloid components). The accurate functioning of this system guarantees the success of the final response and, in the last instance, the survival of the animal.

Amygdalo-hypothalamic relationship: a main conserved association system in tetrapods

Abundant physiological evidence in amniotes indicates that the amygdala profoundly influences a variety of visceromotor responses, as well as the expression of instinctive and conditioned behaviours with a motivational and/or emotional component that could be mediated, at least in part, by projections from the amygdala to the hypothalamus and lower brainstem (Price et al. 1987; LeDoux, 1992; McDonald, 1998; Swanson & Petrovich, 1998). In addition, the strong amygdalo-hypothalamic connections through the stria terminalis constitute one of the important features of the organization of the amygdaloid system in all tetrapods (Risold et al. 1997; Lanuza et al. 1997, 1998; Martínez-Marcos et al. 1999; Moreno & González, 2005b, 2006). Given its importance, studies regarding the connectivity of the AC in different vertebrates used the analysis of the amygdalo-hypothalamic projections to establish putative homologies among amygdaloid territories. In addition, the precise mode in which the amygdala connects with the hypothalamus is of particular interest in evolutionary studies as it seems to be extremely conserved across tetrapods (Bruce & Neary, 1995; Lanuza et al. 1997, 1998; Martínez-Marcos et al. 1999; Moreno & González, 2005b).

In mammals nearly every nucleus projecting to the hypothalamus through the stria terminalis sends fibres to the ventromedial area (Swanson & Petrovich, 1998). These projections arise primarily from the medial amygdala and some nuclei of the basolateral complex, thus carrying vomeronasal, olfactory and multimodal information (Canteras et al. 1995; Petrovich et al. 1996; Risold et al. 1997; Swanson & Petrovich, 1998). The amygdalo-hypothalamic connections control relevant functions mediated by the hypothalamus in response to pheromones and odours (Halpern, 1987; Halpern & Martínez-Marcos, 2003). In mammals, the stria terminalis is a long and prominent fibre bundle that courses from the temporal lobe to the medial telencephalon. Only later, amygdalo-telencephalic and amygdalo-hypothalamic connections branch off from the stria terminalis (Alheid et al. 1995; Petrovich et al. 1996; Risold et al. 1997). Recent studies have shown that similar organization of the amygdalo-hypothalamic projections can be recognized in reptiles and pointed out that this fibre system constitutes one of the best conserved features in the amniotic prosencephalon (Lanuza et al. 1997; Martínez-Marcos et al. 1999). Thus, in lizards the stria terminalis has vomeronasal and multisensorial components arising from areas homologous to its counterparts in mammals, the MeA, posterodorsal ventricular ridge (PDVR) and the LA (Lanuza et al. 1997; Martínez-Marcos et al. 1999).

The situation in birds is more complicated because the lack of a well-developed olfactory/vomeronasal system as a consequence of the reorganization of the secondary centres in the telencephalon (fundamentally amygdaloid), which makes the comparison more difficult (Reiner & Karten, 1985). In addition, many discrepancies exist between the different authors about the subdivisions in the brain in birds, but a recent effort has been made to present a revised nomenclature of the avian brain that helps the comparisons and thus the establishment of homologies (Reiner et al. 2004). Regardless, hodological studies of the telencephalon have shown that from the described avian amygdala hypothalamic projections exist that are comparable with those of mammals. This amygdalo-hypothalamic connection uses the tract termed the 'tractus occipito-mesencephalicus, pars hypothalami', which conveys the descending projection of the arcopallium and amygdala to the hypothalamus (Zeier & Karten, 1971). This tract could represent the stria terminalis but its precise components are uncertain (Reiner et al. 2004). The recently defined 'posterior amygdala' (Reiner et al. 2004) projects multimodal information to the ventromedial hypothalamus (Martínez-García et al. 2002) and the nucleus taenia, which receives olfactory information (Reiner & Karten, 1985) and shows similarities with the MeA (Reiner et al. 2004), sends substantial projections to the ventromedial hypothalamus through the putative stria terminalis of birds (Cheng et al. 1999), therefore reflecting the situation found in other amniotes.

In anurans, most of the amygdalo-hypothalamic projections course through the stria terminalis (Moreno & González, 2005b, 2006). The main similarity with amniotes is the projection to the hypothalamus from comparable amygdaloid territories carrying vomeronasal, olfactory and multimodal information (Moreno & González, 2003, 2004, 2005b). In addition, it should be noted that in anurans shortly after leaving the amygdala, the stria terminalis forms a rostral branch that connects the amygdala with other telencephalic areas and a caudal branch that reaches the ventral hypothalamus (Moreno & González, 2003, 2004, 2005b). This peculiar situation might be due to the lack of pallial displacements that would create something comparable with the temporal lobe. However, it seems reasonable to use the term 'stria terminalis' to define the main amygdaloid efferent system, as in other tetrapods, for which comparable amygdaloid–septal and amygdaloid–hypothalamic components have been described (Alheid et al. 1995; Lanuza et al. 1997; Risold et al. 1997; Martínez-Marcos et al. 1999; Dong et al. 2001). Therefore, although less well organized in amphibians than in amniotes, the presence of a stria terminalis with vomeronasal, olfactory and multisensorial components is a shared feature of tetrapods but its rostral and caudal components vary among vertebrates (Amaral et al. 1992; Stefanacci et al. 1992; Font et al. 1995; Pitkänen et al. 1995; Andreu et al. 1996; Petrovich et al. 1996; Lanuza et al. 1997; Risold et al. 1997; Martínez-Marcos et al. 1999; Dong et al. 2001; Moreno & González, 2003, 2004, 2005b, 2006). All these data show that the precise organization of the forebrain–hypothalamic connections is not exclusively found in amniotes and would serve to segregate important control functions also in amphibians (Fig. 5).

Is there an amygdaloid complex in fish?

The telencephalon of teleosts has a characteristic appearance, with solid paired telencephalic lobes separated by a single median and dorsal telencephalic ventricle covered by a dorsal choroid tela. The current model of the organization of the telencephalic lobes of actinopterygians is based on the eversion hypothesis, which states that the lobes originate by an outward dorsolateral bending of the embryonic telencephalic walls, followed by the expansion of the tela (see Northcutt & Braford, 1980; Northcutt & Davis, 1983; Butler, 2000; Striedter & Northcutt, 2006). In terms of embryonic origin, it seems clear that also in this group of fish four pallial fields and a subpallial ventral region can be detected (see Wullimann & Mueller, 2004). In studies on the evolution of the AC, recent data provided for teleosts are relevant for our understanding of the origin of these structures.

It should be noted that a discrete vomeronasal organ is not present in fish and it is suggested that the early tetrapods were probably the first animals to have separate
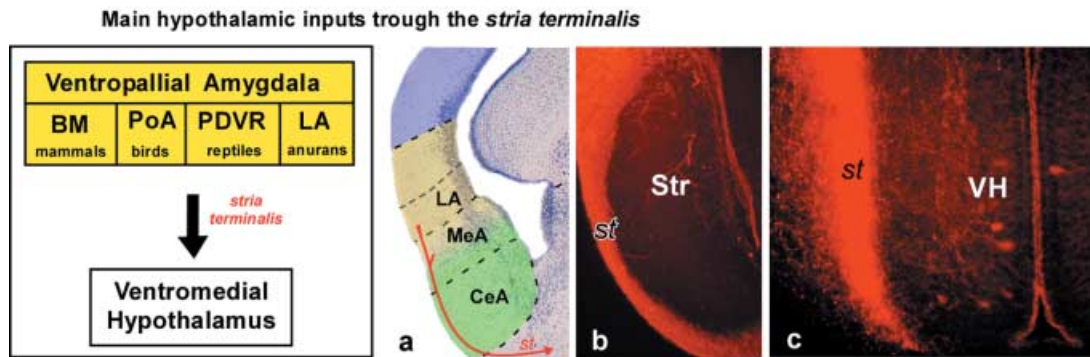
Fig. 5 Schematic diagram of the main amygdaloid nuclei in the different tetrapods projecting to the ventromedial hypothalamus through the stria terminalis. (a) Drawing over a representative transverse section of *Xenopus laevis* at amygdaloid levels illustrating the amygdaloid areas that send their axons through the stria terminalis. (b,c) Representative sections of *Rana perezi* showing by means of tract-tracing techniques (using BDA as tracer and a red fluorescent–streptavidin complex to visualize) the stria terminalis at telencephalic (b) and ventromedial hypothalamic (c) levels.

olfactory and vomeronasal organs (Eisthen, 2004). Thus, a reasonable hypothesis would be that the secondary centres related to this system probably do not exist in fish, are extremely reduced or are exclusively implicated in the olfactory system. However, although teleosts do not have a vomeronasal organ, the olfactory epithelium contains two types of olfactory receptor neurons, ciliated and microvillar, that morphologically correspond to the receptor neurons of the main olfactory mucosa and to the vomeronasal organ of land vertebrates, respectively (see Yamamoto, 1982). Moreover, genes of the vomeronasal olfactory receptor family are expressed in cells of the olfactory epithelium of teleosts (Asano-Miyoshi et al. 2000).

Hodological data in teleosts indicate that a region of the subpallium receives primary and secondary olfactory fibres (Matz, 1995; Folgueira et al. 2004) and projects to other subpallial regions, the hypothalamus and the posterior tubercle (Shiga et al. 1985; Folgueira et al. 2004), resembling the case of the MeA in anurans (Moreno & González, 2003). This evidence does not support a clear homology with the vomeronasal amygdala of tetrapods but at least suggest the existence of an 'early amygdaloid area' in the subpallium of fish (at least as a field homology) (Folgueira et al. 2004). Therefore, the acquisition of a real vomeronasal amygdala would have taken place in the ancestral amphibians.

As previously mentioned, the actinopterygian brain is the result of the eversion process instead of the evagination that other vertebrates undergo and, thus the teleostean mediodorsal pallium would correspond to the lateroventral pallium of 'evaginated brains' (Fig. 6). This assumption is corroborated by the expression pattern of different pallial markers that are highly conserved in evolution (for a review see Wullimann & Mueller, 2004). However, in terms of connections, in anurans this area is one of the main olfactory secondary centres (Moreno & González, 2004), whereas in teleosts it only receives scarce olfactory fibres, being the posterior part of the dorsal portion of the main secondary olfactory area (Folgueira et al. 2004). This ventropallial area in tetrapods gives rise in the adult to the main pallial amygdaloid subdivisions (Puelles et al. 2000; Brox et al. 2004; Medina et al. 2004; Moreno et al. 2004) that, in general, are implicated in emotional memory (LeDoux, 2000). In this sense, the comparable area in teleosts has been demonstrated to be involved in this kind of emotional behaviour (Braford, 1995; Broglio et al. 2005). Notably, however, recent evidence suggests that the posterior telencephalic region that represents the main olfactory centre could also posses a pallial origin and has been embryologically related to the rostral portion (Northcutt, 2006).

Summarizing, in fish the lack of a vomeronasal system was a consequence of the lack of an actual vomeronasal amygdala, which first originated in the next evolutionary step, the ancestral amphibians, but the primordium of this structure could probably be represented in the brain of fish. The amygdaloid area implicated in emotional memory, which seems crucial for survival, most probably evolved before the ancestral amphibians. The existence of an emotional amygdaloid area derived from the latero-ventral pallial areas in fish strongly supports the hypothesis of the current view of the amygdaloid evolution based on recent data in anurans (Moreno & González, 2006) in which the ventral pallial amygdala has been postulated as the multisensorial amygdala implicated in this emotional labelling of stimuli; however, further functional data are needed, at least in anurans.

With regard to the subpallial or pallial origin of the 'vomeronasal amygdala' in tetrapods, the situation found in fish, in which a subpallial region is related to the olfactory system and the hypothalamus (Folgueira et al. 2004), would favour the subpallial origin, whereas the pallial nature of the emotional amygdala would be a general feature shared also by fish (Broglio et al. 2005) (Fig. 6). However, it should be borne in mind that in diverse teleosts, the telencephalon undergoes different
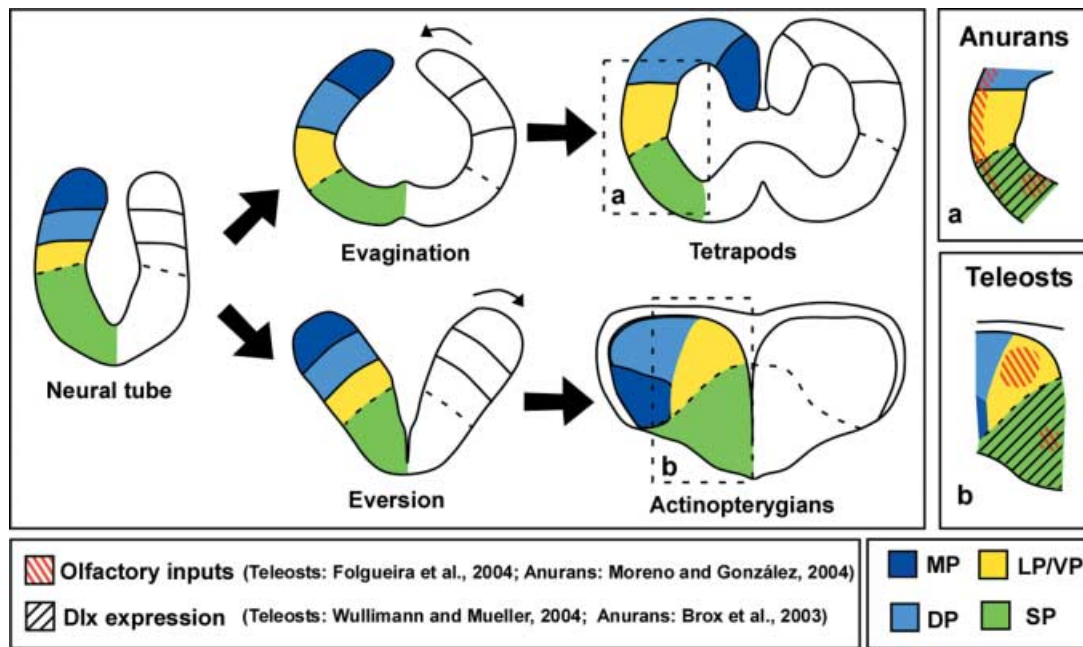
Fig. 6 Schematic representation of the evagination and eversion processes that occur in the telencephalon of tetrapods (a) and actinopterygian fishes (b) during embryonic development showing in the same colour code the relative position of the main pallial and subpallial regions. The localization of the olfactory inputs in the telencephalon of anurans and teleosts is indicated in relation to the expression area for the Dlx genes.

degrees of eversion, as well as distinct patterns of neuroblast migration from the ventricular zone of the telencephalic vesicle. Therefore, homologies between the telencephalic centres of teleosts and land vertebrates, which have paired tubular ('inverted') telencephalic lobes, are still not clear (Northcutt, 1995).

Concluding remarks and evolutionary perspectives

The classic hypothesis regarding brain evolution postulated more than 100 years ago by Edinger proposed that telencephalic evolution occurred in progressive stages of increasing complexity and size, culminating with the human cerebrum. Edinger suggested that the stages proceeded in a ventral-to-dorsal direction, with each new vertebrate group acquiring a more advanced cerebral subdivision. First, there was the 'old brain' (the subpallium at the telencephalic base), which controlled instinctive behaviour, followed by the addition of a 'new brain' (the pallium at the top of the telencephalon), which controlled learned and intelligent behaviour (Edinger, 1908). It is true that this and other classic hypotheses have been criticized and there are many shades of opinion. Nevertheless, evidence is increasing regarding the existence of a basic plan, *bauplan*, in the origin, regionalization and organization of the vertebrate forebrain that makes this classic hypothesis only vaguely reasonable (Puelles & Rubenstein, 1993, 2003; Striedter, 1997; Marín et al. 1998a,b,c; Pombal & Puelles, 1999; Wullimann & Puelles, 1999; Puelles et al. 2000; Smeets

& González, 2000; Bachy et al. 2001, 2002a,b; Martínez-García et al. 2002; Brox et al. 2003, 2004; Moreno et al. 2004; Moreno & González, 2006).

Attending to all the data on the organization of the AC, it seems that at least four key features of the organization of this complex are shared by tetrapods: (1) it is formed by pallial and subpallial derivatives; (2) it is topographically situated in the ventrolateral caudal telencephalic hemispheres; (3) it is strongly related to the olfactory and vomeronasal systems; and (4) it is the origin of important hypothalamic projections. However, in amniotes, the different subdivisions of the AC were proposed on the basis of their distinct connectivity (Bruce & Neary, 1995; Swanson & Petrovich, 1998; Martínez-García et al. 2002): those with long descending projections, those receiving olfactory information, those that do not receive direct olfactory information but that project to the hypothalamus, and those receiving ascending thalamic information. Following the same hodological scheme, three main amygdaloid subdivisions have been identified in anurans (Scalia et al. 1991; Neary, 1995; Moreno & González, 2003, 2004, 2005a,b; Moreno et al. 2005). However, whereas in amniotes separate amygdaloid subpopulations receive olfactory projections and others project to the hypothalamus, in anurans only one ventropallial structure appears to receive direct olfactory information and projects massively to the ventral hypothalamus through the stria terminalis (Moreno & González, 2003, 2004; Moreno et al. 2005). During the evolution of tetrapods the pallium in amniotes, and especially in mammals, was enormously expanded
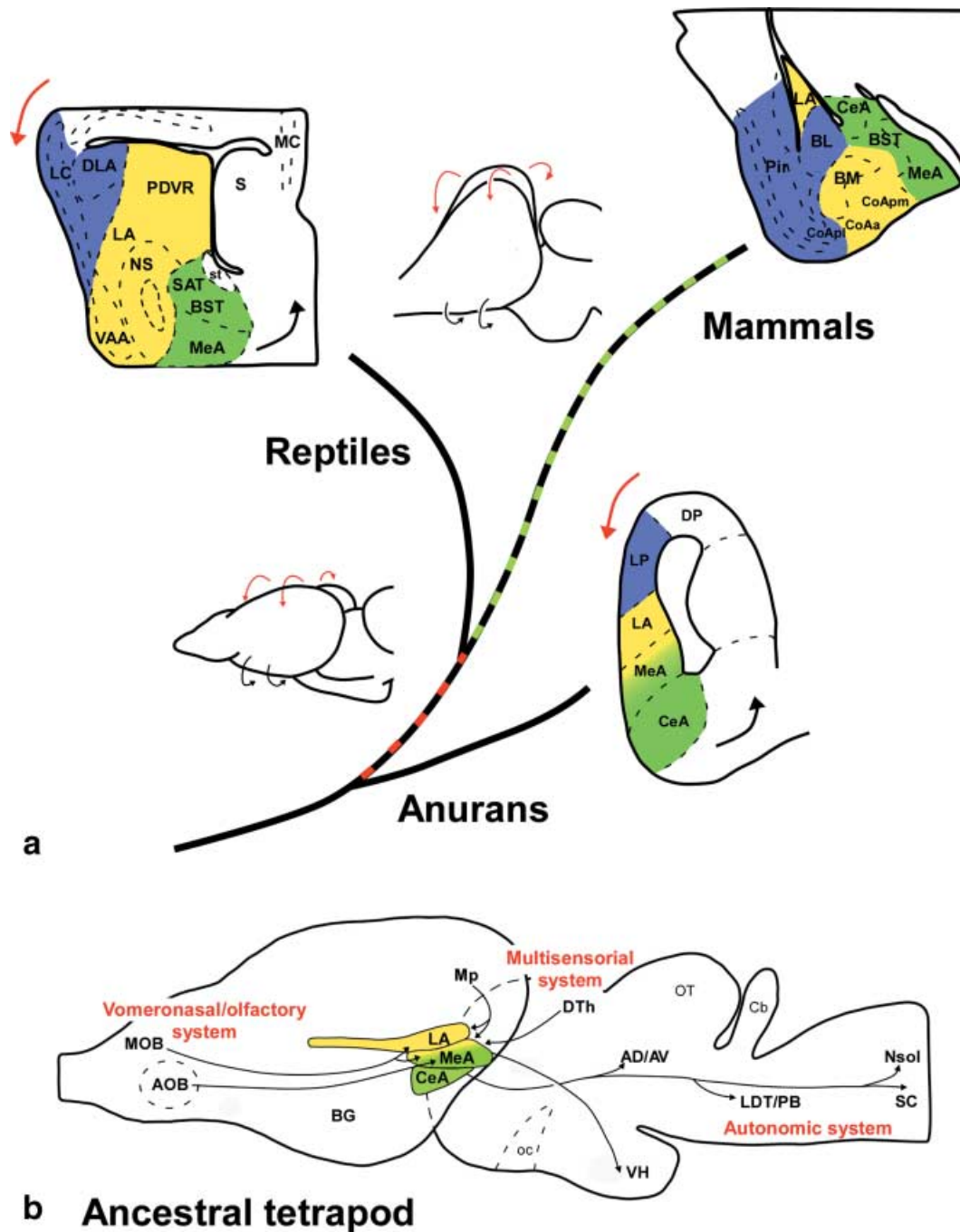
Fig. 7 (a) Phylogenetic tree indicating that during evolution, in the anamnio-amniotic transition (red dashes) the pallial wall of amniotes expanded in a manner such that the dorsal, lateral and ventral pallial regions dramatically increased in size (red arrows). As a consequence the current spatial arrangement of the mammalian amygdaloid complex is the result of an involution of the central, medial and basolateral nuclei (black arrows), which in the ancestral condition (still found in living anurans) occupied a ventrolateral position in the caudal telencephalon, and the acquisition of large areas not present in the ancestral brain. In this view, these 'new evolutionary nuclei' pushed the 'more conserved nuclei' (green dashes), explaining why, in mammals, the central and medial nuclei occupy the most medial position, followed by the basolateral complex, still present in anurans, while the cortical amygdaloid nuclei occupy the most lateral position. Thus, the mammalian amygdala consists of an evolutionarily old centromedial and basolateral region and evolutionarily cortical new regions that are missing in the anuran brain. (b) Amygdaloid connections and main amygdaloid functional systems in the putative ancestral tetrapods inferred from a comparative analysis of the amygdaloid organization. (Diagrams of amniotes are modified from Martínez-García et al. 2006.)

and, thus, the medial, dorsal, lateral and ventral areas dramatically increased in size. As a consequence of the acquisition of large new areas, the current spatial arrangement of the mammalian AC would be the result of a re-localization of the central, medial (autonomic, vomeronasal) and basolateral (primary olfactory) nuclei, which in the ancestral condition occupied a ventrolateral position in the caudal telencephalon, as can be still found in living anurans (Fig. 7). These 'new evolutionary nuclei' (cortical regions) would have pushed the 'more conserved nuclei', explaining why in mammals the central and medial nuclei occupy the most medial position, followed by the basolateral complex, whereas the cortical amygdaloid nuclei occupy the most lateral position. Thus, the mammalian amygdala might be composed of evolutionary old centromedial and basolateral regions and cortical new regions that would be missing in the anuran brain. Additionally, the available data on this system in fish support this hypothesis in that if amygdaloid regions exist (see above), they would possess subpallial and ventropallial origin.

The present revision of the amygdaloid organization in the main vertebrates, in the light of recent findings, includes current knowledge regarding the anuran AC that strongly supports the idea that a basic plan is shared by tetrapods, in which a fundamental scheme can be distinguished sharing functional systems. In non-amphibian anamniotes it seems that during the transition from water- to land-based animals, the brain of ancestral tetrapods developed an elaborated amygdaloid complex in response to the new requirements, and the basic organization of this brain system is still recognizable in all extant tetrapods.

Acknowledgements

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